

MONITORING STUDIES OF THE BENTHIC ECOLOGY OF WAITEMATA HARBOUR, NEW ZEALAND

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Abstract. Changes in a benthic community off Cheltenham Beach were monitored following the rapid die-off of a dense, subtidal (5 m depth) bed of the introduced Asian date mussels (*Musculista senhousia*). Die-off was followed by a 6-9 month flush of bivalves and polychaetes, which thrived on the nutrient-rich muddy substrate that had built up around the mussels. These high abundances of opportunistic suspension- and deposit-feeders were replaced by a short flush of the predatory and scavenging mud crab (*Macrophthalmus hirtipes*). Benthos diversity and density progressively declined over a 2-3 year period as the muddy substrate disappeared and the pre-existing sand beneath was exhumed. The muddy substrate of the mussel bed supported a fauna substantially different and richer than that in the background sandy substrate (twice the diversity, five times the density, abundant worms).

Three and a half years of monitoring an initially dense bed of native horse mussels (*Atrina zelandica*) at 14 m depth in Rangitoto Channel indicated rapid growth during their first 3-4 years (35 mm/month length increase). This was followed by the virtually complete loss of the bed over a 2-3 year period (from a density of 200-300/m² to 1-35/m²), possibly a result of storm scour, shell damage and subsequent predation, or carrying capacity being exceeded as individuals grew.

Two and a half years of monitoring recently re-established intertidal seagrass circles (*Zostera novozelandica*) at Cox's Creek showed mean monthly radial growth rates of 150 mm/month with no significant seasonal variation. If this is the start of the return of flourishing seagrass beds to the Waitemata Harbour shores (lost through a fungal outbreak 50-60 years ago), then it will take several more decades to develop extensive beds.

Monthly monitoring of populations of the introduced small semelid bivalve *Theora lubrica* in a low tidal muddy habitat in Hobson Bay revealed considerable variation in density (30-850/m²). During 24 months of monitoring, six cohorts were identified based on the seasonal change in the size composition. These showed slower growth rates and longer-lived populations in cooler months (0.5 mm/month, 6-8 months longevity) than in the summer (2-3 mm/month, 2-3 months longevity). Significant die-offs occurred in spring in both years, but the very low densities of summer 1997-98 were not matched in the summer of 1998-99 when the highest densities were recorded.

Cores showed that the majority of *Theora lubrica* live 10-30 mm below the surface of the substrate. Studies of size distribution of populations at different tidal heights provided no evidence of any migration up or down the shore as they mature. Controlled feeding trials showed that the mud crab *Macrophthalmus hirtipes* is a major predator of *Theora lubrica*, with one crab capable of consuming up to seven of these small bivalves/

day. Monitoring revealed an apparent correlation between high crab numbers and low *Theora* densities and suggested that crab predation could control *Theora* density.

KEYWORDS: New Zealand, Auckland, Waitemata Harbour, monitoring, ecologic change, *Musculista senhousia*, *Atrina zelandica*, *Zostera novozelandica*, *Theora lubrica*, introduced marine species.

INTRODUCTION

Of New Zealand's many splendid harbours, the Waitemata Harbour (Fig. 1) in Auckland (Lat 36° 50' S Long 174° 45' E), is the most utilised and impacted by human activities. It is the busiest port in the country, has the most intensely industrialised and densely populated catchment (c. 750 000), and is the playground for the country's largest city. It is also home to the largest number of introduced exotic marine organisms in New Zealand (66 species, Hayward *et al.* 1999). It is imperative that we better understand the ecology of the harbour and the impacts of introduced species, so that we can monitor the harbour's health in the face of pollution, increased sediment and freshwater runoff, and the threat of additional marine introductions.

The small monitoring studies documented here have evolved out of the results of larger scale subtidal and intertidal surveys (Hayward *et al.* 1997, 1999) undertaken when most of the authors were either employed by, or volunteers at, the Auckland War Memorial Museum.

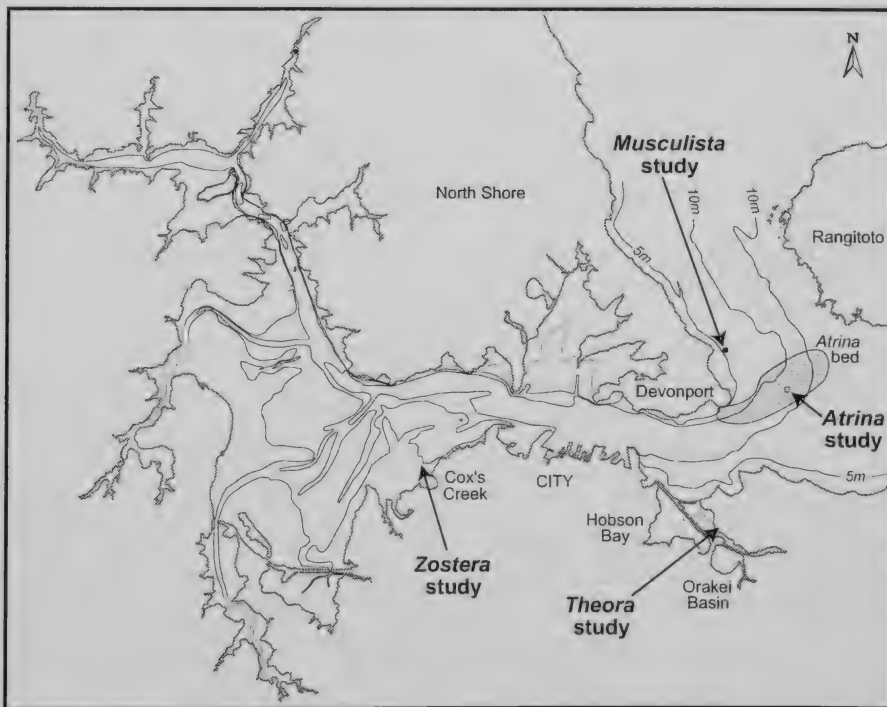


Fig. 1. Location in the Waitemata Harbour of monitoring sites for our studies of: an Asian date mussel (*Musculista senhousia*) off Cheltenham; a horse mussel bed (*Atrina zelandica*) in the Rangitoto Channel; seagrass (*Zostera novozelandica*) at Cox's Creek; and the small semelid bivalve (*Theora lubrica*) in Hobson Bay.

PART 1—RECOVERY OF A SUBTIDAL ECOSYSTEM FOLLOWING DIE-OFF OF AN ASIAN MUSSEL INFESTATION

(by BWH, ABS, MSM, HRG, WMB)

INTRODUCTION

The small Asian mussel, *Musculista senhousia*, was first discovered in New Zealand in the Waitemata Harbour about 1978 (J.E. Morton pers. comm., Willan 1985). Within a decade it spread as far north as Parengarenga and south to East Cape, but does not appear to have extended its range since then (Willan 1985, 1987; Morley 1988). It lives in patches (5 m²-10 ha) that accumulate thick mud drifts over the shallow subtidal and low tidal seafloor in many parts of the Waitemata Harbour (Hayward *et al.* 1997, 1999; Hayward & Hayward in press). These beds are continually dying off, with new patches being established each year (Creese *et al.* 1997).

During a reconnaissance survey of the subtidal, soft bottom benthos of the Waitemata Harbour in July 1993, one dredge station taken in 5 m of water off the north-west end of Cheltenham Beach, Devonport (Fig. 1), encountered a muddy thicket of live mature *Musculista senhousia*. Its existence as an extensive bed was confirmed by diving observations (S. Hooker pers. comm. 1993) and a further dredge haul taken in November 1993. The station was resampled by dredging in February 1994, and subsequently monitored with further sampling in June and September 1994 (one sample each) and in August 1995, January and September 1996, and February 1997 (with four replicate dredge samples). The February 1994 sample encountered only dead shells of *Musculista senhousia*, suggesting a die-off of the bed, which was confirmed by subsequent sampling (although two live specimens were recorded in June 1994) and by a further diving inspection (S. Hooker pers. comm. 1995).

A serendipitous result of these dredge surveys and monitoring has been the documentation of the recovery of an area of seafloor and its biota, following its colonisation for approximately two years by a dense mat of introduced Asian date mussels and the resulting accumulation of a thick drift of mud. In New Zealand the impact of Asian mussel beds on the native ecosystem has previously been documented in intertidal situations in the Tamaki Estuary (Creese *et al.* 1997).

METHODS

The subtidal station was relocated each time with an accuracy of ± 20 m using satellite GPS and local landmarks. Samples were hand-hauled from a 4 m dinghy powered by a small outboard motor using a naturalist's dredge with 10 litre capacity. The dredge sampled 60-100 mm into the seafloor sediment and generally came up 90-110% full, having sampled 0.15 m² of seafloor sediment. In most instances the dredge bit deeply into the relatively soft substrate and needed to be dragged only a few metres across the sea floor before being filled. Each sample was washed over a 1 mm sieve to remove mud and sand, and the residue was fixed with preservative. In the laboratory all preserved live organisms were hand picked, identified, and counted.

The results were tabulated (Appendix 1) and the occurrence through time of the more common taxa graphed to illustrate the faunal change after the die-off of the *Musculista* (Figs 2, 3).

RESULTS

Dredge samples of the thicket in July and November 1993 had scaled densities of live Asian mussels of 150-200/m² of sea floor. These densities are relatively low compared with those

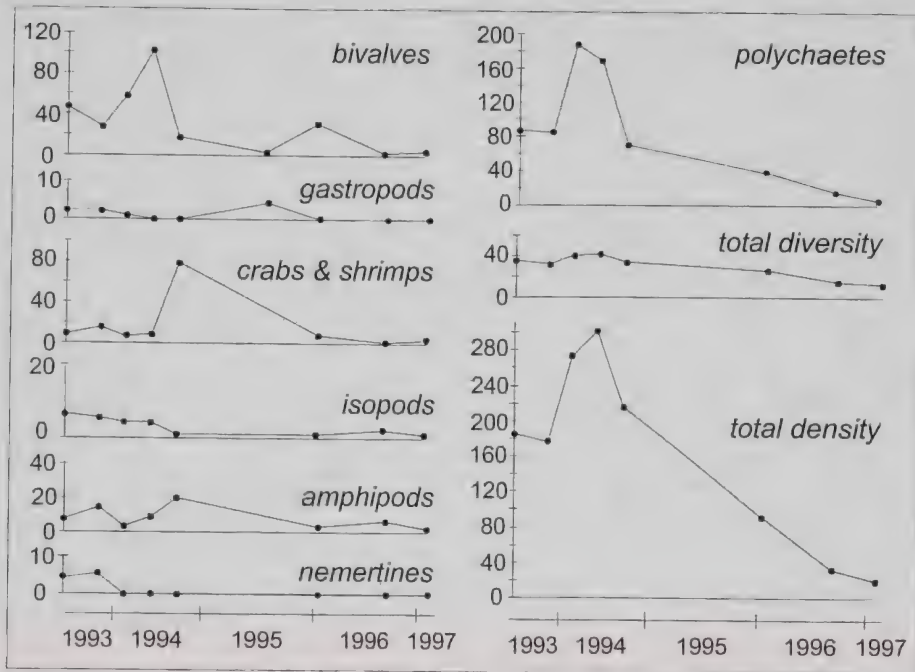


Fig. 2. Graphs showing changes in abundances of seven faunal groups, overall diversity (number of species) and overall density (total number of individuals) following the die-off of an Asian mussel thicket in the subtidal monitoring station off the west end of Cheltenham Beach, from July 1993 to February 1997.

recorded in some intertidal situations around the Waitemata (Creese *et al.* 1997, Hayward & Hayward in press). The last record of living mussels ($10/\text{m}^2$) was in June 1994. The mussels in the thicket mostly died off during the summer of 1993-94 and the thicket broke up and washed away in the months that followed. The dredged sediment noticeably changed from dominantly mud in 1993 to cleaner sand several years later.

A simple diversity curve (number of species present) indicates 32-36 species/ 0.15 m^2 were living in the thicket (Fig. 2); it increased slightly to 41-43 species during the nine months following die-off; then progressively decreased to less than half that diversity (13-15 species), 30-36 months following die-off. A very similar pattern is seen in the density curve (number of individuals). The thicket supported c. $1200 \text{ individuals}/\text{m}^2$, which increased to 1800-2000 in the 3-6 months after die-off, and then progressively decreased to 150-250, 30-36 months after die-off. The major contributors to these diversity and density curves are the polychaete worms and to a lesser extent the infaunal bivalves, which show parallel results (Fig. 2).

Nemertine worms and isopods were both more numerous in the thicket than following its die-off. Gastropod and amphipod numbers show only minor variations throughout the monitoring period. Decapod crustacea (crabs and shrimps) have slightly higher densities in the thicket than in the sand 36 months later, with an unusual peak density nine months after die-off (Fig. 2), produced by a flush ($500/\text{m}^2$) of the mud crab, *Macrophthalmus hirtipes* (Fig. 3).

Species abundance curves (Fig. 3) show that many species (e.g. polychaetes—*Axiobella quadrimaculata*, *Glycera lamellipoda*, *Paprionospio*, *Prionospio*, *Terebellanice*, Capitellidae; the amphipod *Torridoharpina hurleyi*; the isopod *Natalolana albicaudata*; the holothurian *Trochodota*

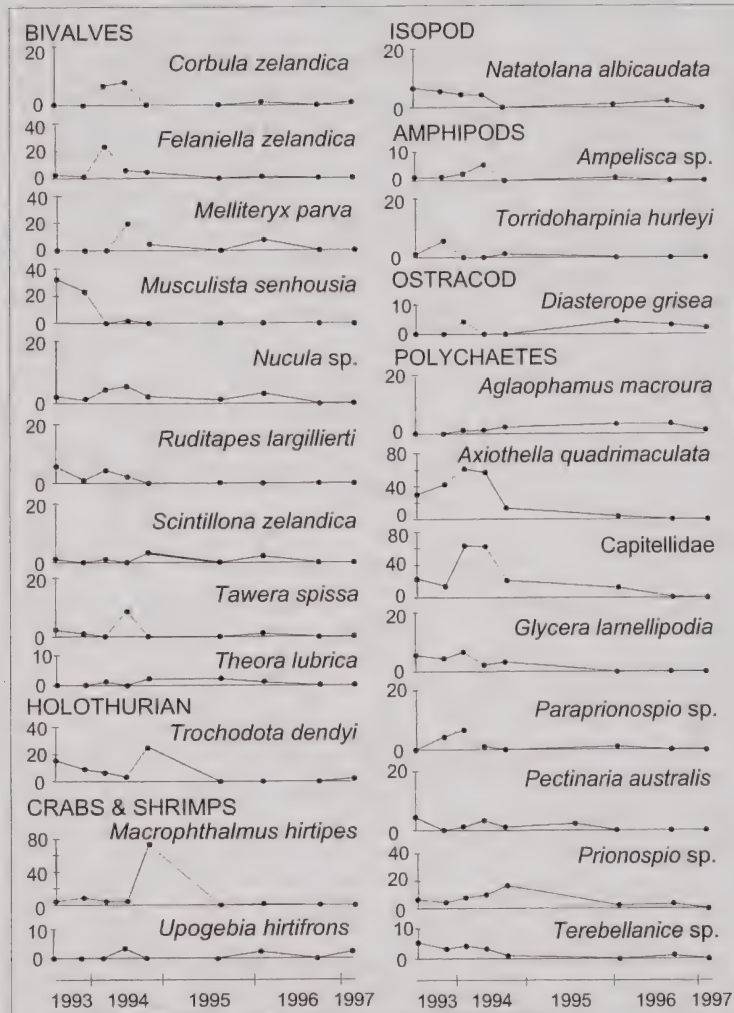


Fig. 3. Graphs showing species abundance changes following the die-off of an Asian mussel thicket in the subtidal monitoring station off the west end of Cheltenham Beach, from July 1993 to February 1997.

dendyi) had considerably greater abundances in the muddy thicket than in the sand substrate, 30-36 months after die-off.

Species that were not recorded living in the thicket and with significant, but patchy, abundances thereafter, include the bivalves *Corbula zelandica*, *Felaniella zelandica*, *Melliteryx parva*, *Theora lubrica*; the shrimp *Upogebia hirtifrons*; ostracod *Diasterope grisea*; and polychaete *Aglaophamus macroura*.

Many species had a peak abundance in the 3-6 months following die-off, including the bivalves *Corbula zelandica*, *Felaniella zelandica*, and *Tawera spissa*; the amphipod *Ampelisca* sp.; and the polychaetes *Axiobella quadrimaculata*, *Paraprionospio* sp., and *Capitellidae*. Several species (e.g. the holothurian *Trochodota dendyi*; the polychaete *Prionospio*; and the crab *Macrophthalmus hirtipes*) had their peak abundance nine months after die-off.

DISCUSSION

Studies of intertidal Asian date mussel thickets show them to have a non-uniform patchy distribution; they live for about two years and many die off during the higher temperatures of mid summer. As the thicket ages and dies it progressively erodes away (Creese *et al.* 1997). The subtidal thicket off Cheltenham exhibited a similar pattern, although we can only infer the mussels were about two years old when they died.

Our monitoring of the recovery of a subtidal site following the die-off of an invasive mussel bed also documents the impact of the mussel bed on the original ecosystem, assuming that the site had fully recovered to its original state after 30–36 months. The byssal threads of the Asian date mussels accumulate mud, which builds to a depth of 50–150 mm and grossly modifies the character of the substrate. This appears to have an adverse impact on some of the infaunal, suspension-feeding bivalves (e.g. *Corbula zelandica*, *Felaniella zelandica*, *Melliteryx parva*) and possibly the large carnivorous polychaete *Aglaophamus macroura*, but resulted in an increase in the diversity and density of the fauna overall, as mud-loving organisms colonised and flourished (e.g. the holothurian *Trochodota dendyi*, many polychaetes, the isopod *Natatolana albicaudata*, and the amphipod *Torridoharpinia hurleyi*).

The sessile, filter-feeding Asian date mussels gather and spill numerous food particles, which accumulate around them, together with excreted material, as high-nutrient mud. The die-off of mussels was closely followed over the next 6–9 months by a flush of suspension—and deposit-feeding juvenile infaunal bivalves (*Corbula*, *Felaniella*, *Melliteryx*, *Tawera*, *Nucula*), large amphipods (*Ampelisca*) and polychaetes (*Axiobella*, *Paraprionospio*, *Prionospio*), which rapidly colonised the newly available nutrient-rich substrate. This flush of opportunistic animal life coupled with warmer spring temperatures, probably resulted in a flush of the predatory and scavenging mud crab (*Macrophthalmus hirtipes*) recorded nine months after mussel die-off. The mud crab peak was accompanied by a corresponding decrease in the abundance of many of the opportunistic prey species.

Diversity and density of most organisms progressively fell to a relatively low, stable level 30–36 months after the mussel die-off, as the relatively clean sand substrate was re-established.

PART 2—DYNAMICS OF A SUBTIDAL HORSE MUSSEL BED

(by BWH, ABS, MSM, HRG)

INTRODUCTION

When Powell (1937) surveyed the subtidal benthos of Waitemata Harbour in the 1930s, he recorded no live horse mussels (*Atrina zelandica*). It was therefore surprising that our reconnaissance dredge survey of the same area in July 1993 showed an extensive horse mussel bed in muddy fine sand covering a triangular area between south Rangitoto, Bean Rock, and Devonport (Fig. 1; Hayward *et al.* 1997). The bed was most dense and extensive on the outside of the bend of the main harbour channel, and one station here in 14 m of water (Fig. 1) was chosen to monitor the growth rate and life span of the mussels. The station was resampled by dredging in November 1993, February, June and September 1994 (one sample each) and in August 1995, January and September 1996, and February 1997 (with four replicate dredge samples).

This horse mussel “invasion” of the Waitemata Harbour was a natural, rather than a human-assisted phenomenon. Horse mussel beds are transitory (Grant-Mackie 1987) and the Waitemata Harbour bed was no exception. The density of live specimens decreased progressively with very

few live mussels left by mid 1996. In 1995 and 1996 huge volumes of horse mussel shells were washed up on nearby beaches during storms.

METHODS

Field methods of station location, dredging, sieving and preservation were the same as in the study on Asian date mussels. In the laboratory, the live horse mussels were sorted into 10 mm size classes, based on the length of their shells, and counted. Because of the relatively shallow depth of penetration of the dredge, many of the larger horse mussels had their beak ends cut off and their total lengths were estimated using the tapering shape of their shells.

RESULTS

The mean length of the horse mussels increased from 118 mm in July 1993 to 166 mm in September 1994 giving a mean annual growth rate of 41 mm/yr (3.5 mm/month). The mean size then remained static for the next 18 months and probably 2.5 years, although numbers dredged after January 1996 were insufficient for an accurate assessment (Fig. 4).

The density of horse mussels in the study site progressively decreased over time from 150-200/m² in July and November 1993 to 80-100/m² a year later, to 40/m² another year later and to 2-5/m² by August 1996 and February 1997 (Fig. 4).

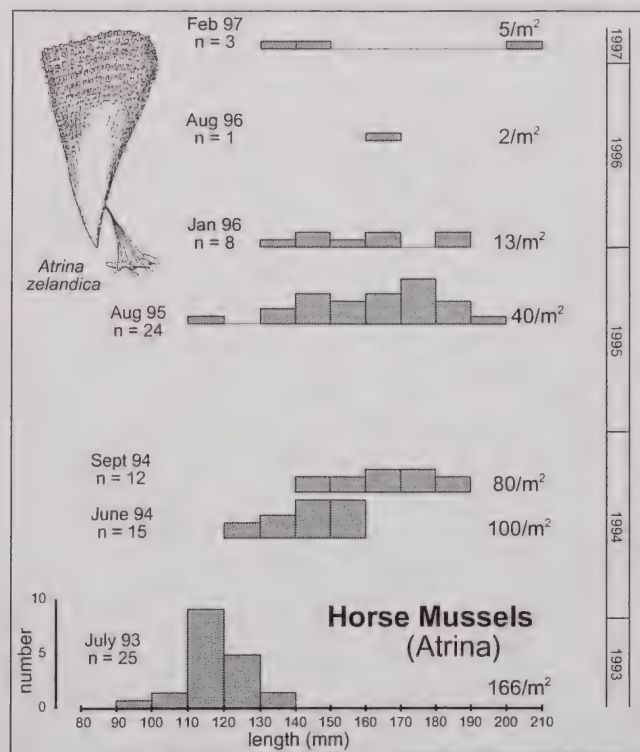


Fig. 4. Histograms showing size distribution of horse mussels during each sampling of the bed north of Bean Rock, from July 1993 to February 1997. The number of specimens measured (n) and density (n/m²) are also given.

DISCUSSION

As sample sizes are relatively small, conclusions from our results are tentative. If the horse mussels grew in their early years at the same rate they did during the study, then the population was three years old when monitoring began in July 1993. This population appears to have started dying off at 3.5 years in age and this continued for the next 2.5 years with resulting progressive decrease in density. After six years there were very few horse mussels alive. The large drifts of horse mussel shells washed up along Auckland's East Coast Bays in 1995 and 1996 were undoubtedly derived from the die off of this large bed and possibly other beds further north that had settled 4-5 years earlier.

We can only speculate as to the cause of the die off. Grant-Mackie (1987) attributed a similar die off in beds north of the present study area to storms eroding the subtidal substrate. Many horse mussels were "washed-out" and others suffered shell damage which allowed predators such as whelks to attack the soft parts (Grant-Mackie 1987). Horse mussels are the principle host to the pea-crab *Pinnotheres atrinocola* and specimens were recovered from horse mussels in this study. At no stage, however, did we record high incidences of crab infestations, such as those noted in McLay (1988), and so we do not infer pea-crab parasitism as contributing to the dynamics of our horse mussel study population.

Our monitoring results suggest that the horse mussels grew rapidly for the first four years of their lives, after which growth virtually stopped or certainly slowed dramatically. We know of no other published growth rates for *Atrina zelandica*, although Cameron Hay undertook detailed measurements on tagged individuals in the Marlborough Sounds for 4.5 years in the 1980s. He recorded rapid growth in their first two years with large shells at least five years and possibly up to 15 years old (C. Hay pers. comm.).

PART 3—RETURN OF INTERTIDAL SEAGRASS PATCHES

(by BWH, KAH, JJH, MSM)

INTRODUCTION

The tidal flats around the fringes of the central Waitemata Harbour were formerly covered in green seagrass, *Zostera novozelandica*, a marine angiosperm, but it was virtually wiped out in the Auckland region by a fungal outbreak 50-60 years ago (Armiger 1964, Dromgoole & Foster 1983). *Zostera* roots help stabilise the substrate and the plant is reputed to improve water quality in polluted habitats.

The only area in the harbour with substantial seagrass beds in the 1990s was the southern shore between Meola Reef and the harbour bridge. Here, at and below MLWS, large areas of soft sand are clothed in seagrass. During intertidal shoreline surveys in the mid and late 1990s, we noted that small circles of seagrass seemed to be reappearing on the tidal sand flats in several places around the Waitemata Harbour (e.g. Orakei Basin, Okahu Bay, St Heliers, Karaka Bay). One of the greatest concentrations of small seagrass circles was found between mid and low tide at the mouth of Cox's Creek, Herne Bay (Fig. 1). This site was selected to monitor the circles to investigate whether they provided any evidence of the return of the former seagrass cover and to document their seasonal and annual growth rates.

At Cox's Creek we observed that fine sand and silt builds up around the binding roots of the seagrass so that the substrate is often softer than the surrounding area. Dead cockle shells are caught by the seagrass, accumulating into thick drifts which in places bury and kill off parts of the circles. New circles form by vegetative propagation—a broken runner from an existing

patch is swept to a new site by the tide and sends down roots thus establishing the nucleus of a new patch. New branching runners grow radially outwards forming a circular patch.

METHODS

A pace and compass plan of the seagrass circles near the mouth of Cox's Creek was prepared on 7 March 1996 (Fig. 5). Each circle was assigned an identification letter which was used throughout the monitoring. During each monitoring visit, two diameters of each circle were measured with a tape measure, one parallel to the sea shore and the other perpendicular to it. The circles were remeasured in August and October 1996, January, March, August and October 1997, and April and October 1998. New small circles that became established within the study area during the monitoring were progressively added. The plan of the seagrass circles was redrawn at the conclusion of monitoring in October 1998 (Fig. 5). Results of the monitoring of each circle diameter were graphed as radial growth rates (Fig. 6). Mean monthly radial growth rates for all circle diameters have been calculated for each of the intervals between measurements.

RESULTS

During the monitoring period all circles increased in size by outwards radial growth. There was no significant difference in growth rates in any direction—an observation supported by the circular to near-circular shape of all patches. Several of the circles increased in size and coalesced with adjacent ones (Fig. 5). During the 31 months, total area of the intertidal *Zostera* circles increased by 150% (from 2400 m² to 6000 m²).

The mean monthly radial growth rate for all *Zostera* circles for the 31 months of monitoring

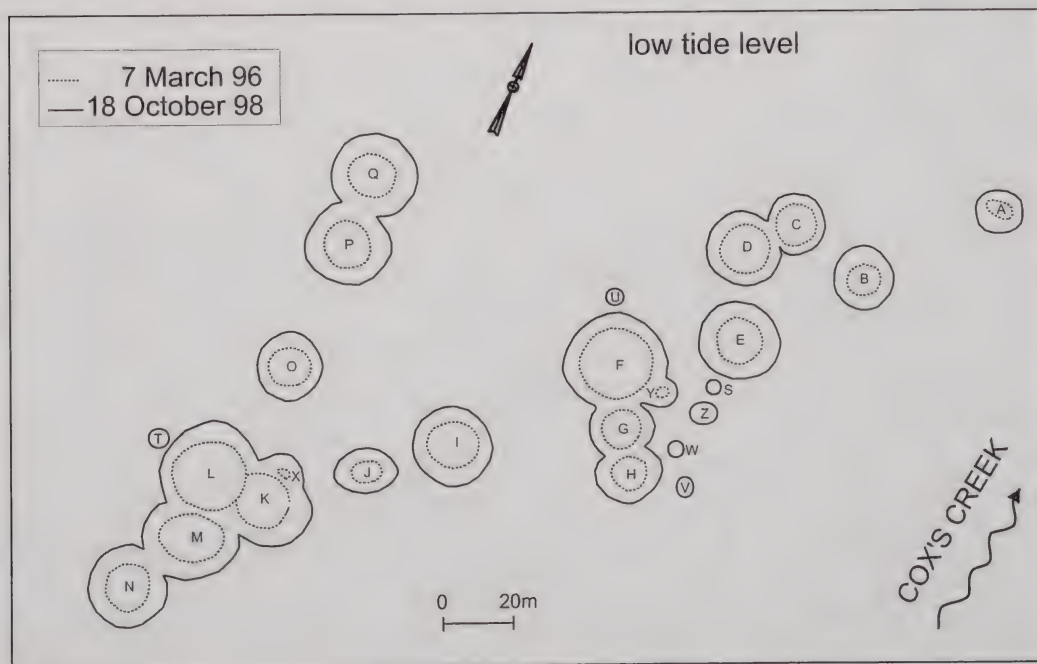


Fig. 5. Plan of seagrass circles (A-Q, S-Z) between mid and low tide levels at Cox's Creek at the start and finish of the growth monitoring programme from March 1996 to October 1998.

was 150 mm/month. The period of most rapid growth (mean 210 mm/month) was early spring 1996 (Aug.-Oct.) and slowest growth (mean 90 mm/month) was late summer 1997 (Jan.-Mar.). In early spring 1997 (Aug.-Oct.), the mean growth rate was 120 mm/month and over summer (Oct. 1997-Apr. 1998) it was 130 mm/month.

The plot of increasing diameters of individual *Zostera* circles (Fig. 6) indicates that while there is considerable variability, the overall growth rate over the full 31 months is remarkably consistent. There does not appear to be any consistent seasonal or other pattern. Growth rate projections suggest that the largest circle in 1998 (F—30 m diameter, Fig. 5) was nine years old.

DISCUSSION

Studies on the growth of *Zostera* in Australia have shown marked seasonal variability with maximum biomass in summer and minimum in winter, with biomass differences between the two seasons ranging between two and 40 times (e.g. Kerr & Strother 1990, McKenzie 1994). Similar major seasonal changes in the apparent health and cover of *Zostera* have been noted in Manukau and Parengarenga Harbours in New Zealand (pers. obs. M. Morley, F. Thompson respectively). It appears that once established, seagrass beds display these seasonal patterns of abundance and growth. Our monitoring did not investigate seasonal biomass variability and focussed on the growth rates of the runners and shoots as measured by radial increase in size of the circles. It is still surprising however that we did not find any significant seasonality in their growth rates.

Long-time local residents of Cox's Creek recall that in the 1940s and 1950s most of the

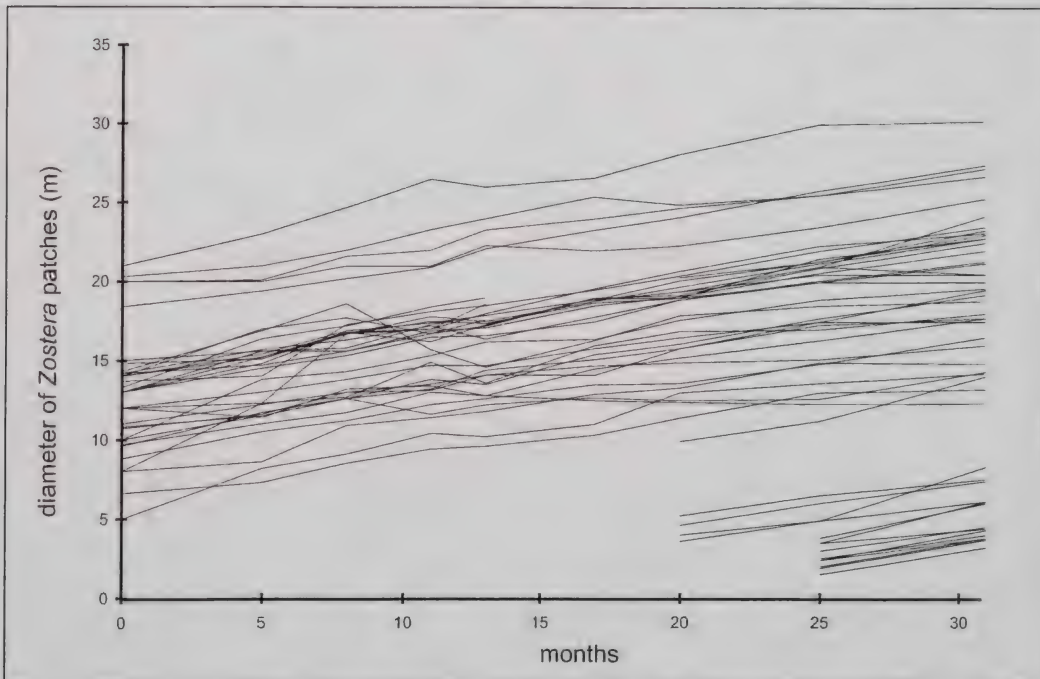


Fig. 6. Graph showing the trend of increasing diameters of seagrass circles (two diameters at right angles measured/circle) during the monitoring programme. Diameter measurements on new seagrass circles that became established during the monitoring appear at bottom right.

intertidal flats were covered in thick seagrass. One anonymous local resident believes that the extensive seagrass of the past dated from a time of extensive sewerage pollution of the bay, before establishment of the Mangere Sewerage Plant. He has also noted the return of seagrass in recent years and correlates it with periodic sewerage overflows into Cox's Creek. He says he has noted some sewerage washing up around the Cox's Creek coast at high tide level; the recent establishment of flourishing seagrass patches at this unusually high tide level (not part of this study) may be correlated with the sewerage nutrients. It is far less certain that sewerage overflows into Cox's Creek have anything to do with the return of the *Zostera* circles at lower tide levels. Low-tide *Zostera* have been noted returning in several places around the harbour and many are not at sites of known sewerage overflows.

Of all the harbours in northern New Zealand, the one with the most extensive intertidal seagrass beds is Parengarenga. Here the intertidal substrate is mostly clean quartz sands and its catchment is a mix of scrublands and low intensity pastoral farmland. Parengarenga probably has the lowest levels of anthropogenic nutrient input of any of the northern harbours and appears to be a direct contradiction to the supposed link between seagrass vitality and high nutrients.

If major seagrass beds are indeed returning to the Waitemata Harbour, the growth rates we have documented suggest that it could take several more decades to achieve.

PART 4—POPULATION DYNAMICS OF A SMALL INTRODUCED SEMELID BIVALVE

(by MSM, BWH)

INTRODUCTION

The small, thin-shelled Asian semelid bivalve *Theora lubrica* (maximum length 15 mm), arrived in the northern harbours of New Zealand about 1972, probably in ship ballast water from its home in Japan (Climo 1976, Dromgoole & Foster 1983). It has since spread to most other ports in the country (Hayward 1997). In recent decades, *Theora lubrica* has become the dominant mollusc in mud and muddy sand in the extensive low tidal and shallow subtidal flats throughout most of the Waitemata Harbour (Hayward *et al.* 1997). It seems that *Theora lubrica* can rapidly colonise disturbed and muddy habitats and is perhaps the most pollution-tolerant mollusc in the harbour, living in the contaminated sediments of the Westhaven marina, beneath the Auckland wharves and in the Tamaki Estuary (Hayward *et al.* 1997, M. Morley pers. obs.).

Since it is a new arrival, and now a major member of the Waitemata Harbour ecosystems, it is of interest to find out what impact *Theora lubrica* may be having on the native species and what attributes of its biology have allowed it to colonise so rapidly and successfully these foreign shores.

The life history of *Theora lubrica* has been investigated in its native habitats in Japan (e.g. Tanaka & Kikuchi 1979, Imabayashi & Wakabayashi 1992), but this could differ in its new home. We decided to investigate and document elementary aspects of its life history—growth rate, life span, timing of spawning and density in the substrate.

STUDY SITE

The study site in Hobson Bay (Fig. 1) was easily accessible from the road; but seldom visited by the public (i.e. too muddy). It was exposed at low tide for at least 1-2 days every fortnight, and had sufficient area of substrate to allow for multiple quadrat sampling over many months, without needing to resample the same substrate twice in any one six month period.

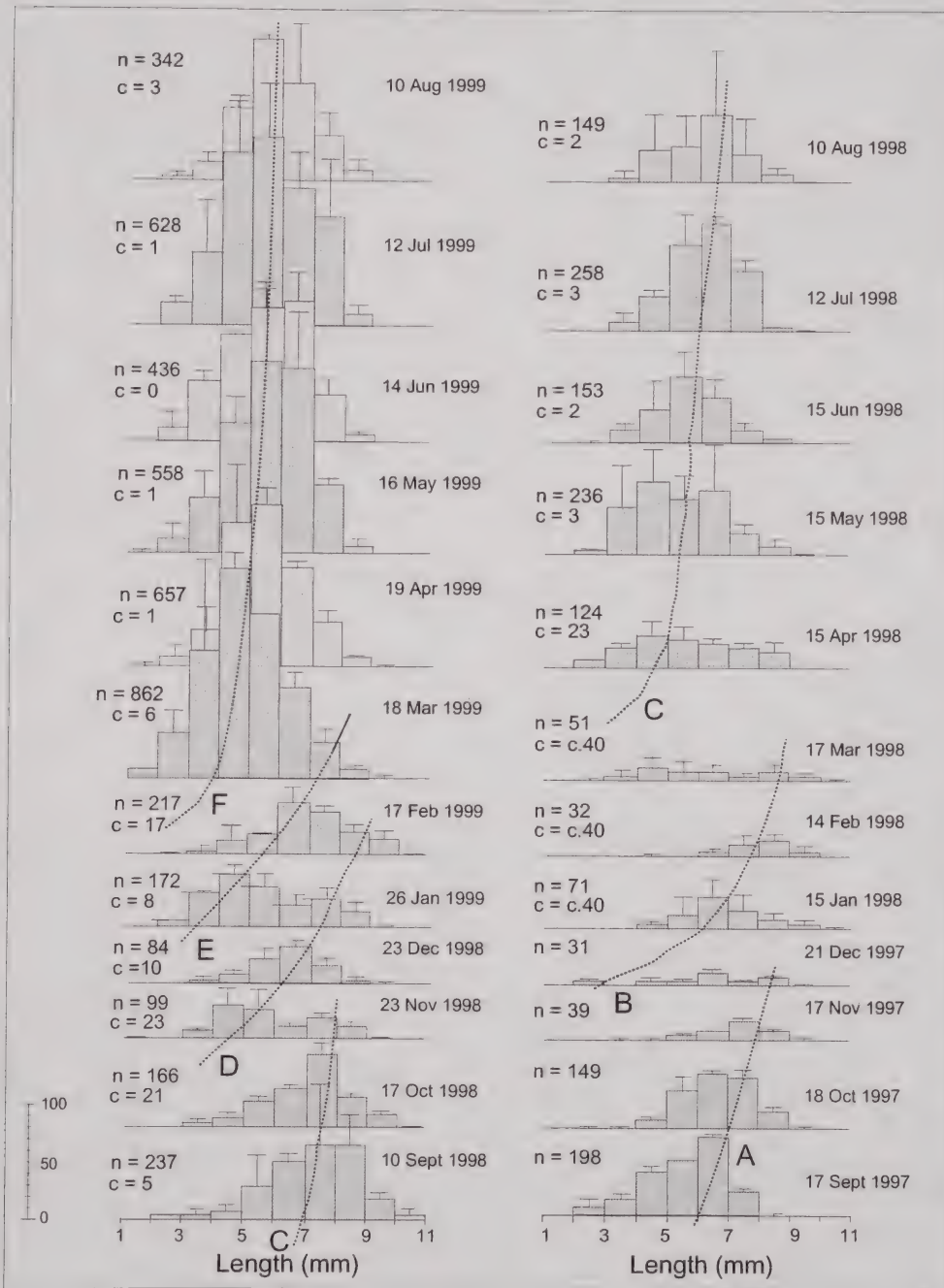


Fig. 7. Histograms showing the monthly size distribution (shell length in mm; frequency expressed as a mean of two replicate samplings of 0.5 m²) and density (number, n/m²) of low tidal *Theora lubrica* from Hobson Bay, from September 1997 to August 1999. Bars show standard deviation of numbers in each size class between two replicate quadrat samplings. Dashed lines show interpreted mid-point of successive cohort populations (A to F). Number of crabs, *Macrophthalmus hirtipes* (c) per m² is recorded after January 1998.

The study site is on the south side of Purewa Creek estuary where it enters Hobson Bay, 100 m north of Orakei Railway Station. It is immediately seaward of the mud-covered (50-100 mm thick) intertidal tuff rock platform at a tidal height of 0.7 m.

METHODS

The site was visited during a spring low tide every month for 24 months, from September 1997 to August 1999. On each visit, two 0.5 m² quadrats were marked on the surface of the mud at approximately the 0.7 m tidal height. In each quadrat the mud was excavated with a spade to a depth of 100 mm and washed on site through a large sieve with 1 mm openings. The coarse fraction retained on the sieve was taken home and all live *Theora lubrica* were sorted into 1 mm size classes based on their shell length and counted. Because of their slim, elongate shape, most *Theora* less than c. 2.5 mm long passed through the sieve.

RESULTS

The monthly patterns of size distribution and change (Fig. 7) were always similar in both quadrats, although density between the two quadrats sometimes varied (resulting in larger standard deviations). During our first year of monitoring *Theora* densities, we observed low densities through the warmer summer months (November 1997 to March 1998, 30-70/m²) and higher densities through the cooler late autumn to spring months (May to October 1998, 150-250/m²). The significant drop in density in spring (September to November) of 1997 also occurred in spring (November-December) 1998. The low densities throughout the summer of 1997-98 (December to March) were not repeated in the summer of 1998-99; instead densities progressively increased reaching peak densities of 850/m² in March 1999.

Visual inspection of the size histograms (Fig. 7) suggests six cohorts during our 24 months of monitoring. These are labelled as A-F (Fig. 7) and show that spawning occurs intermittently throughout the year with significant recruitments identified in pre-September 1997 (A), December 1997 (B), March 1998 (C), November 1998 (D), January 1999 (E) and March 1999 (F).

Monthly monitoring of these cohorts indicates that *Theora* have the fastest growth rates in the warmer summer months (c. 2-3 mm/month) and the slowest growth rates through the cooler winter months (c. 0.5 mm/month). The largest *Theora* recorded were in the 10-11 mm length class, with the majority reaching only 9-10 mm. Summer cohorts (B, D, E) appear to live for only 2-3 months, whereas the winter cohorts (C, F) lived for 6-8 months.

DISCUSSION

With warmer sediment temperatures than in New Zealand, even more dramatic die offs of *Theora* have been recorded in summer in Japan and related to temporary oxygen-deficient conditions (Tanaka & Kikuchi 1979). We have no evidence of a similar cause for the Hobson Bay die-back in the 1997-98 summer. It may be related to increased predator pressure and/or a period of low spawning or locally poor settlement.

In the shallow seas of *Theora*'s native range in Japan, its maximum growth rates (6 mm/month), maximum observed density (2000/m²) and maximum shell size (13-16 mm) are greater (Imabayashi & Wakabayashi 1992) than those observed here. Despite this, there are parallels between the populations in their native land and in their new home. In both places, spawning and recruitment occur intermittently all year, summer cohorts are shorter lived than winter (6 months), growth rates are faster in summer than winter, and significant die-backs may occur in warmer months.

PART 5—SUBSTRATE DEPTH AND INTERTIDAL DISTRIBUTION OF LIVE *THEORA LUBRICA*

(by BWH, MSM)

INTRODUCTION

An important aspect of understanding the ecology and population dynamics of the small introduced semelid bivalve, *Theora lubrica*, is knowledge of how deep it lives within the soft muddy substrate. We could find no published records of this. *Theora* has relatively long thin siphons and is a deposit-feeder. This implies that it probably lives near the surface and no deeper than the length of its extended siphons.

As they mature, some intertidal bivalves are known to migrate to lower tidal levels or even into shallow subtidal depths (e.g. Redfearn 1974, Douglas 1982). If this phenomenon occurs in *Theora lubrica* then it will impact on our interpretation of its population dynamics which we have based on monitoring at a single site (Part 4), c. 0.7 m above extreme low water spring (ELWS) level.

METHODS

The depth to which *Theora* live at our study site in Hobson Bay was investigated during a spring low tide when numbers of individuals were at their peak (3 April 1999). A short length of PVC pipe (36 mm diameter) was pushed into the surface sediment to take short cores. After extraction from the mud, each core was progressively extruded, using a plunger from beneath,

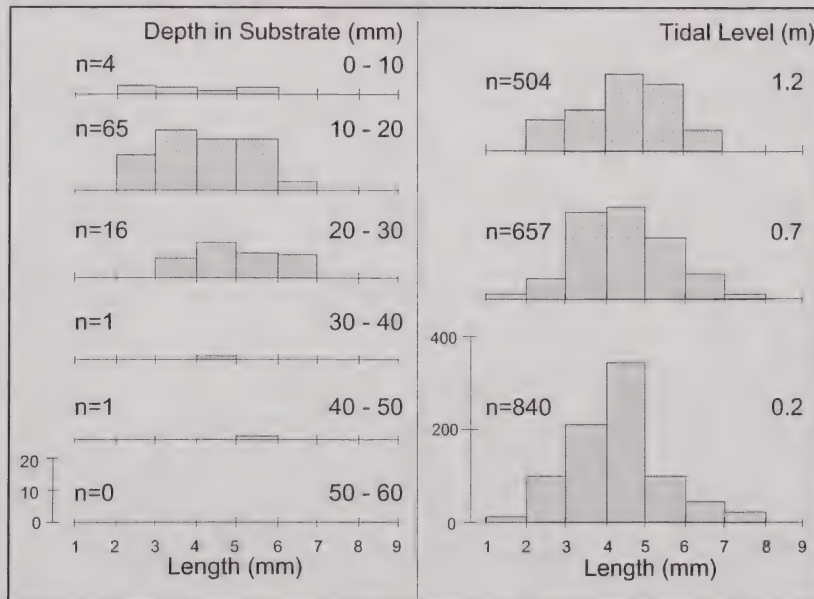


Fig. 8. Left: Histograms showing the size distribution and density (number, $n/0.03 \text{ m}^2$) of low tidal *Theora lubrica* from Hobson Bay, at 10 mm intervals in the mud to a depth of 60 mm; results are the total from two replicates on 3 April 1999. Right: Histograms showing the size distribution and density of *Theora lubrica* at different tidal levels (m above ELWS) on the shore of Hobson Bay on 19 April 1999 (results standardised to number, n/m^2).

so that 10 mm thick slices could be cut off and processed separately, down to a depth of 60 mm. After 15 cores had been taken (0.015 m²), the combined sediment slices from each 10 mm depth interval were washed through a sieve with 1 mm openings. The coarse fractions retained on the sieve were taken home and all live *Theora lubrica* were sorted into 1 mm size classes based on their shell length and counted. A replicate sampling of another 15 cores was also taken.

To investigate whether *Theora* migrate up or down the shore as they mature, their size distribution and abundance were measured at three tidal levels during our usual monthly sampling on 19 April 1999, when bivalve abundances were at their peak. The two usual 0.5 m² monthly quadrats were sampled, together with two additional quadrats at tidal heights 0.5 m above and below (1.2 m and 0.2 m) our main study level (0.7 m). In horizontal distance these were 10 m up and down slope from the main site.

RESULTS

No live *Theora* were recorded deeper than 50 mm and only two were recorded deeper than 30 mm (Fig. 8). Over 95% of the live *Theora* were present in the upper 30 mm of sediment, with 60% present at 10–20 mm and 30% at 20–30 mm depth. Few *Theora* were present in the upper 10 mm. The smallest *Theora* (2–3 mm) tend to live at shallower depths than the largest individuals (6–7 mm).

In the Waitemata Harbour, the mean difference between spring and neap low tides is about 0.7–0.8 m. Examination of tide charts indicate that our lowest site at 0.2 m above ELWS is exposed at spring low tide for less than an hour about 6–8 times/year; our main study level at 0.7 m is exposed during low tide on about half of the tides; and our highest site at 1.2 m is exposed at low tide on every tide, for periods of 1–5 hours. Thus our lowest site is essentially shallow subtidal for most of the time.

Our studies showed no significant difference in *Theora* size structure at these three different tidal levels (Fig. 8). Our results suggest a slightly increasing density with distance down the shore (Fig. 8).

DISCUSSION

Some 90% of *Theora lubrica* live 10–30 mm below the surface, with very few deeper than 30 mm. They may burrow deeper when the tide is out. As these measurements were undertaken at low tide, it is possible that *Theora* could live slightly shallower when the substrate is immersed in water.

Our studies suggest that there is no significant migration up or down the shore as *Theora* mature. As our lowest sampling site was essentially subtidal, there is no evidence of movement into the local subtidal zone either. The slightly increased density at lower tidal levels possibly relates to the shorter exposure time during tidal cycles.

PART 6—CRAB PREDATION OF *THEORA LUBRICA*

(by JJH, BWH)

INTRODUCTION

Early results from the monitoring of the population of the introduced bivalve *Theora lubrica* (Part 4) indicated that in some months there were dramatic population declines (e.g. Oct. to Nov. 1997). Such declines could be natural die-offs with old age, or caused by environmental changes (e.g. high temperature, low oxygen), or predation.

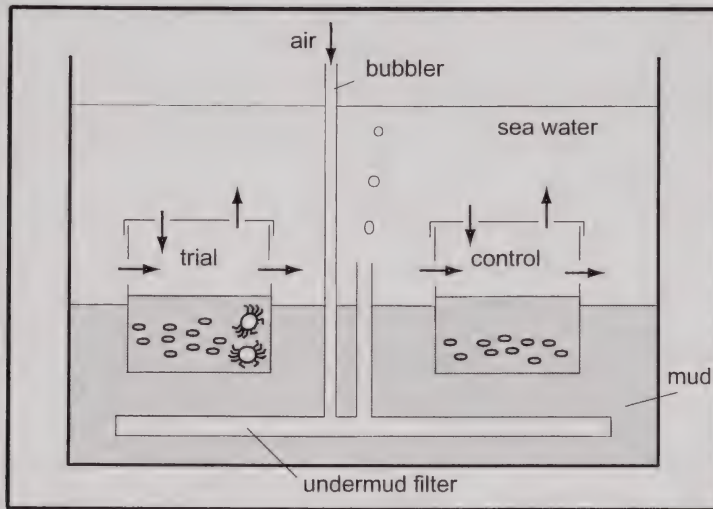


Fig. 9. Diagram of the aquarium for the *Theora lubrica* feeding trials.

Since the decline appeared to be across all size classes, it seemed that old-age was unlikely to be the major cause. We were not monitoring environmental factors, so we focussed on potential predators. Foraging sea-birds are rarely seen in the vicinity of the study site and were therefore unlikely. Bottom-feeding fish (e.g. rays, snapper, flounder) could not be excluded. Within the muddy sediment itself there appeared to be two potential predator species: burrow-dwelling snapping shrimps (*Alpheus richardsoni*) and crabs (*Macrophthalmus hirtipes*). Feeding trials were undertaken in March and April 1998 to investigate the possibility that mud crabs and snapping shrimps might be significant predators of *Theora lubrica*.

METHODS

A small salt-water aquarium was established containing five 150 mm-diameter plastic containers with lids and an aerating bubbler (Fig. 9). The containers and their lids were perforated to allow for water circulation. Mud, collected from the monitoring site in Hobson Bay, was pushed through a sieve with 2 mm openings to remove all crabs, shrimps or sizeable *Theora*, and then placed in the bottom of the aquarium and plastic containers to a depth of c. 80 mm. The aquarium, with containers, was then filled with sea water to a depth of c. 150 mm and left to settle for several days.

Twenty 5-10 mm long *Theora* were placed in each of the five containers and left overnight to burrow into the mud. Next morning one or two potential predators (crabs or snapping shrimps) were placed in each of three containers and the other two were left as predator-free controls.

These feeding trials (with five containers each time) were run three times. After being left undisturbed for 240 hours (2 trials) or 48 hours (1 trial), the mud from each container was passed through a sieve and the number of live *Theora* and crabs or snapping shrimps recorded (Fig. 10).

RESULTS

The four control containers, without crabs or snapping shrimps, retained 80-100% of their

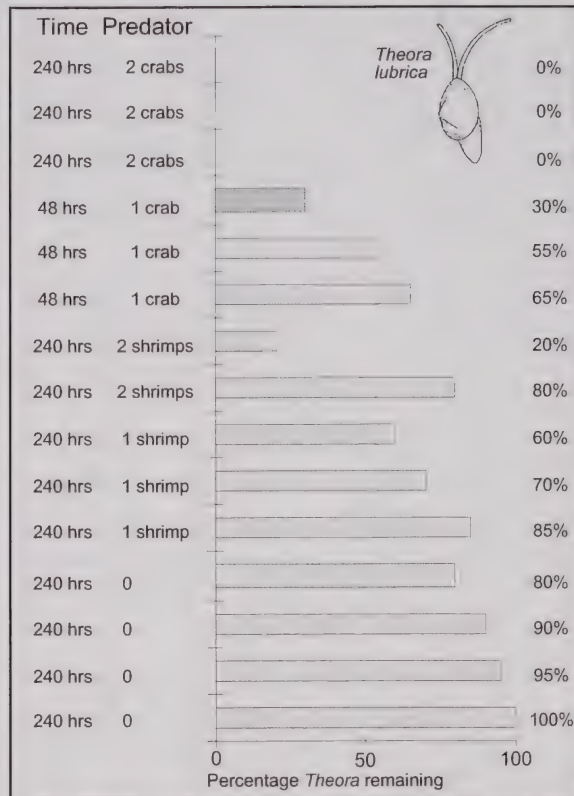


Fig. 10. Bar graphs showing the results of the feeding trials (with controls), to test whether the crab *Macrophthalmus hirtipes* and/or the shrimp *Alpheus richardsoni* feed on the small introduced bivalve *Theora lubrica*.

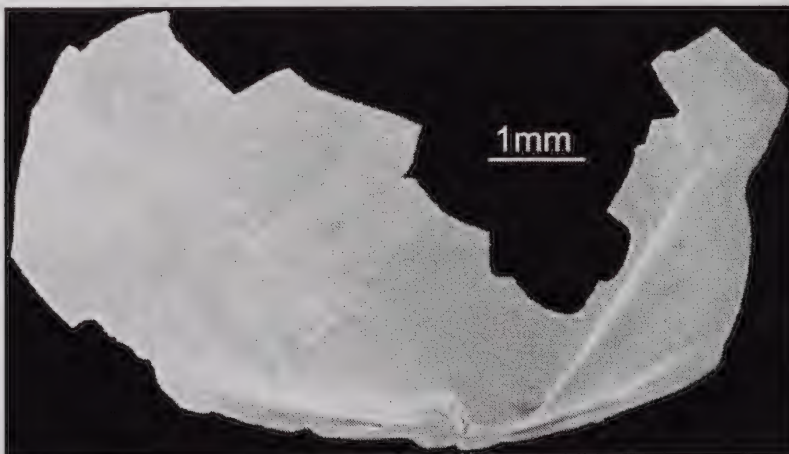


Fig. 11. Scanning electron micrograph of a valve of *Theora lubricica* (recovered from one of our feeding trials) that has been chewed by the chela of the crab *Macrophthalmus hirtipes*.

original 20 live *Theora* after 240 hours (Fig. 10). The three containers with one snapping shrimp each, retained 60-85% of their original 20 live *Theora* after 240 hours. The two containers with two snapping shrimps each retained 20-80% after 240 hours. All three containers with two crabs each, had no live *Theora* remaining after 240 hours. Three containers with one crab each, retained 30-65% of the original live *Theora* after a mere 48 hours. Fragments of thin *Theora* shells with jagged (apparently crushed) edges (Fig. 11) were recovered from some of the containers with crabs, and suggest that the strong crab chelae are easily capable of breaking the *Theora* shells.

After suspecting that crabs might be influencing the *Theora* population densities, we began monthly monitoring of all associated macrobiota in our quadrats in April 1998 (Fig. 7). We recalled relatively high crab numbers (c. 40/m²) for at least the three preceding months. Subsequent monitoring showed the density of the crab *Macrophthalmus hirtipes* fluctuated from a low of 0-3/m² in cooler months (May to August 1998) to a peak of 30-40/m² in warmer months (December 1997 to March 1998).

DISCUSSION

There appears to be a small background loss of *Theora* resulting from their translocation and confinement in the aquarium. Feeding trials using snapping shrimps provided rather variable results that can be interpreted as negligible to moderate predation rates on *Theora*.

Feeding trials using the mud crab *Macrophthalmus hirtipes* provided convincing evidence that they are a major predator of such a small, fragile bivalve. The 240 hour trials show an average minimum feeding rate of one *Theora*/crab/day. The 48 hour trials gave a range of 3.5-7 *Theora* consumed/crab/day. It is possible that the artificial aquarium conditions could have stressed the *Theora*, and made them more susceptible to predation. These consumption rates, if repeated in nature, could account for much of the large population decline sometimes recorded.

During the period of major *Theora* decline in summer 1997-1998, bivalve densities fell over a two month period from 200 to 40/m². At the same time densities of c. 40 *Macrophthalmus* crabs/m² were present in the study quadrats. If all the lost *Theora* resulted from crab predation, the consumption rate would have averaged 0.07 *Theora*/crab/day, well within the crabs' capability documented in our feeding trials. The much higher consumption rate in our feeding trials from that apparent in the wild, may in part be due to the higher density of *Theora* in our trials (1000/m²) and the lack of other replenishing food resources in our trials compared with natural tidal conditions.

These fluctuating densities pose several questions. Are they natural seasonal fluctuations independent of the introduced *Theora*? Is predation by native crabs controlling the density of introduced *Theora*? Is the presence of large densities of the recently introduced food source, *Theora*, increasing densities of crab predators? If so, is this resulting in other downstream effects on the ecosystem?

We have insufficient data to answer most of these questions. Observations elsewhere have shown that crab numbers naturally increase in spring and summer and decline over winter (ABS pers. obs.). Our monitoring shows this same seasonal pattern. This suggests that variations in *Theora* densities are not the primary cause of our observed seasonal variations in crab numbers. The two years of monitoring suggests that higher crab densities (e.g. summer 1997-98) are correlated with lower *Theora* densities (e.g. summer 1998-99) and that to some extent crab predation controls the density of *Theora*.

Acknowledgements. Some of these studies were undertaken with funding from New Zealand Lottery Science and the Auckland War Memorial Museum. All include considerable voluntary input in participants'

own time. For assistance with field work we thank Jenny Riley, Greg Mutu, Julianne Cheetham, Maggie Webb, Ramola Prasad and Laila Moch. We thank Simon Hooker (NIWA) for use of his personal communications on the status of the Cheltenham Beach Asian mussel bed as observed by diving, and Cameron Hay (University of the South Pacific, Solomon Islands) for permission to quote some of his unpublished results on horse mussel growth rates. Bob Creese and Murray Gregory read the manuscript and suggested improvements.

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APPENDIX 1. Census data of live fauna (retained on 1 mm sieve) from monitoring dredge sampling of the subtidal station off the west end of Cheltenham Beach, from 27 July 1993 to 25 February 1997. Expressed as number of specimens/0.15 m² of sea floor. Last four sampling results are the mean of four replicates. Results for 8.8.95 lack data from the 1-2 mm size fraction and are therefore incomplete and not included in the analysis of faunal trends (Figs 2, 3).

Survey date	27.7.93	19.11.93	10.2.94	3.6.94	23.9.94	8.8.95 mean	23.1.96 mean	17.9.96 mean	25.2.97 mean
POLYPLACOPHORA									
<i>Leptochiton inquinatus</i>	0	0	0	0	0	0	1.25	0	0
GASTROPODA									
<i>Austromitra rubiginosa</i>	0	0	0	0	0	1	0	0	0
<i>Cominella adspersa</i>	1	2	0	0	0	0	0	0.25	0.25
<i>Cominella quoyana</i>	0	0	0	0	0	0.5	0.25	0	0
<i>Eatoniella roseola</i>	0	0	0	0	0	0.25	0	0	0
<i>Epitonium minora</i>	0	0	1	0	0	0	0	0	0
<i>Maoricolpus roseus</i>	0	0	0	0	0	0.75	0.25	0	0
<i>Neoguraleus murdochi</i>	0	0	0	0	0	0.5	0	0	0
<i>Philine</i> sp.	0	0	0	0	0	0.5	0	0	0
<i>Trichosirius inornatus</i>	0	0	0	0	0	0.25	0	0	0
<i>Zeacolpus pagoda</i>	0	0	0	0	0	0.75	0	0	0
<i>Zegalerus tenuis</i>	1	0	0	0	0	0	0	0	0
<i>Zemitrella choava</i>	0	0	0	0	0	0.25	0	0	0
BIVALVIA									
<i>Arthritica bifurca</i>	0	0	12	47	2	0.25	11	0	0
<i>Corbula zelandica</i>	0	0	7	8	0	0	1.25	0.5	1.25
<i>Cyclomactra ovata</i>	0	0	0	0	0	0	0	0.25	0
<i>Dosina zelandica</i>	0	0	0	0	0	0	0	0	0.25
<i>Dosinia lambata</i>	0	0	0	1	0	0	0.25	0	0
<i>Felaniella zelandica</i>	2	1	24	6	4	0	1.5	0	0.5
<i>Gari stangeri</i>	0	0	0	0	0	0	0	0	0.25
<i>Leptomysa retiaria</i>	2	0	5	0	0	0.25	0.5	0	0.5
<i>Melliteryx parva</i>	0	0	0	20	5	0	7.5	0	0
<i>Musculista senhousia</i>	32	24	0	2	0	0	0	0	0
<i>Nucula hartvigiana</i>	0	1	2	6	2	0.5	1.75	0.5	0.25
<i>Nucula nitidula</i>	2	0	2	0	0	0.25	1.5	0	0
<i>Pleuromeris zelandica</i>	0	0	0	0	0	0	1.25	0	0.75
<i>Purpurocardia purpurata</i>	0	0	0	2	0	0	0	0	0
<i>Ruditapes largillierti</i>	6	1	4	2	0	0.5	0.5	0.25	0
<i>Scintillona zelandica</i>	1	0	1	0	3	0	2.25	0	0
<i>Tawera spissa</i>	2	1	0	9	0	0	1.25	0.5	0.25
<i>Theora lubrica</i>	0	0	1	0	2	1.75	1	0	0
<i>Zenatia acinaces</i>	0	0	0	0	0	0.25	0.25	0	0.25
OPHIUROIDEA									
<i>Amphiura roseus</i>	0	0	0	0	0	0.25	0.75	0	0
<i>Amphiocnida pilosa</i>	1	0	0	0	0	0.25	0	0	0
<i>Amphiopolis squamata</i>	0	0	0	1	1	0	0.75	0	0
HOLOTHURIA									
<i>Trochodota dendyi</i>	16	9	7	3	26	0.25	0.25	0	2

Survey date	27.7.93	19.11.93	10.2.94	3.6.94	23.9.94	8.8.95 mean	23.1.96 mean	17.9.96 mean	25.2.97 mean
REPTANTIA									
<i>Halicarcinus</i> sp.	0	0	0	0	0	0	0.25	0	0
<i>Halicarcinus varius</i>	1	2	0	0	3	0	0.25	0	0
<i>Helice crassa</i>	0	2	0	0	0	0	0	0	0
<i>Macrophthalmus hirtipes</i>	4	9	4	4	74	0	1	0	0
<i>Notomithrax minor</i>	1	0	0	0	0	0	0	0	0
<i>Paguristes pilosus</i>	0	0	2	1	0	0.75	2.25	0.25	0
<i>Pagurus</i> sp.	0	0	1	0	0	0	0	0	0
<i>Pinnotheres atrinocoloa</i>	0	0	0	0	2	0	0	0	0
<i>Pyromaia tuberculata</i>	0	0	0	0	0	0	0.25	0	0
<i>Upogebia danai</i>	0	0	0	0	0	0	0	0.25	0
<i>Upogebia hirifrons</i>	0	0	0	3	0	0	2.75	0.25	2.75
<i>Upogebia</i> sp.	2	0	0	0	0	0	0	0.25	0
DECAPODA									
<i>Callianassa filholi</i>	0	0	0	0	0	0	0.25	0	0.5
<i>Callianassa</i> sp.	0	0	0	0	0	0	0.5	0	0
<i>Palaemon affinis</i>	1	0	0	1	0	0	0	0.25	0
<i>Pontophilus australis</i>	0	3	0	0	0	0	0	0	0
ISOPODA									
<i>Natatolana albicaudata</i>	7	6	4	5	0	0	0.75	2.25	0.5
<i>Natatolana nammuldi</i>	0	0	0	0	1	0	0	0	0
<i>Natatolana</i> sp.	0	0	0	0	0	0	0	0	0.25
AMPHIPODA									
<i>Ampelisca chiltoni</i>	0	0	0	0	0	0	0	1.25	0
<i>Ampelisca</i> sp.	1	1	2	6	0	0	1	0	0
<i>Corophium sextonae</i>	0	0	1	0	1	0	0	0	0
<i>Elasmopus</i> sp.	1	0	0	2	0	0	0	0	0
<i>Liljeborgia akaroica</i>	0	0	0	0	0	0	0.5	0	0
<i>Maera mastersi</i>	0	0	0	0	0	0	0.25	0	0
<i>Melita awa</i>	0	0	0	1	2	0	0	0	0
<i>Melita festiva</i>	2	0	0	0	0	0	0	0	0
<i>Melita</i> sp.	0	0	0	0	0	0	0	0	0.5
<i>Metaphoxus</i> sp.	0	0	0	0	3	0	0	0	0
<i>Paradexamine pacifica</i>	0	4	0	0	2	0	0	0	0
<i>Paradexamine</i> sp.	0	4	0	0	0	0	0	0	0
<i>Paraperioculodes</i> sp.	0	0	0	0	1	0	0	0	0
<i>Parawaldeckia</i> sp.	0	0	0	0	0	0	0	0	0.25
<i>Parawaldeckia thomsoni</i>	3	0	0	0	2	0	0.25	1.25	1.25
<i>Proharpinia</i> sp.1	0	0	0	0	8	0	1.75	0	0
<i>Proharpinia</i> sp.2	0	0	0	0	0	0	0	3.25	0
<i>Protophoxus australis</i>	0	0	0	0	0	0	0	0.5	0.5
<i>Torridoharpinia hurleyi</i>	1	6	0	0	1	0	0	0.25	0
TANAIDACEA									
	0	0	0	1	0	0	0	0	0
LEPTOSTRACA									
	0	0	0	0	0	0	0.25	0	0
OSTRACODA									
<i>Diasterope grisea</i>	0	0	4	0	0	0	4	3.25	2
<i>Scleroconcha arcuata</i>	0	0	1	0	0	0	0	0	0
Ostracoda indet.	3	7	0	2	0	0	0	0	0

